MARSUPIAL BIOGEOGRAPHY IN RELATION TO CONTINENTAL DRIFT

P. G. Martin

The University of Adelaide, South Australia

CONTENTS

Summary.

1. Introduction
2. Present distribution of marsupials
3. The consideration of other mammals
4. The fossil record
   (a) Summary of the information
   (b) Attitudes towards interpreting the fossil record
   (c) An interim interpretation of the fossil record
5. "Chemical palaeogenetics"
6. Distribution patterns among other organisms
   (a) Introduction
   (b) The south-temperate distribution pattern
   (c) The tropical amphi-transpacific distribution pattern
7. Assessment of hypotheses about marsupial biogeography
   (a) Northern dispersal
   (b) Southern dispersal
   (c) Trans-pacific dispersal
8. Postscript — new geophysical evidence

Summary. — 1. Marsupials occur in America and Australia-New Guinea and, with one exception, their fossils have only been found in these continents. The earliest fossils occur in western North America and they are thought to have spread from there in the late Cretaceous to both western Europe and South America. Their earliest occurrence in Australia is Oligocene. Absences from the fossil records are taken into consideration and hypotheses which discount these absences are rejected until they are shown by new discovery to be feasible.

2. Northern dispersal from North America via Asia to Australia-New Guinea is rejected because Australia moved at least 15° north in the mid-Tertiary. By the time contact with Asia occurred, placentals were well-established there; the exclusion of placentals from Australia, together with absence of marsupials from Asia and Indonesia, rule out northern dispersal.

3. Southern dispersal from South America via Antarctica to Australia is possible but presents the following difficulties:

(i) *Geophysical.* The reconstructions of McKenzie and Sclater (1971), which reveal a landbridge from 75 to 45 m.y.b.p., require further study in the light of evidence
   (a) that Antarctica is composed of at least three tectonic units with separate Mesozoic histories
   (b) that West Antarctica is an archipelago

(c) that the reconstructions lead to the conclusion that *either* South America and Africa moved about 14° south from 75 to 45 m.y.b.p. and then about 14° north from 45 m. y.b.p. to now, *or* an Australian Eocene flora which has sub-tropical characteristics originated inside the Antarctic circle.

(ii) *Biogeographical.* These include :

(a) The difficulty of explaining the exclusion from South America of Australian marsupials, which had evolved to sub-family level by 50 m.y.b.p., and of the great flora of Western Australia.

(b) The difficulty of explaining the exclusion from Australia of placentals, always present at the same time as marsupials in the South American fossil record.

(c) It is necessary to have a different hypothesis to explain the presence of monotremes in Australia.

(d) The " South Temperate biota " has been discussed and it is concluded that P. J. Darlington (1965) made a useful generalisation about it, viz. that most plants and invertebrate groups shared by south-east Australia and southern South America are present in New Zealand. It is concluded that marsupials do not belong to this biota as would be expected if there had been an Antarctic landbridge. It is also concluded that this biota originated in an isolated continent, comprising at least the New Zealand platform and Marie Byrd Land, which was divided at 80 m.y.b.p.

4. The difficulties associated with the northern and southern dispersal routes encourage the consideration of trans-Pacific dispersal by division and drift of a Mesozoic mid-Pacific continent. This is compatible with what we know of the tectonic histories of the north and east Pacific and our present ignorance of the tectonic history of the western Pacific means that the hypothesis cannot be excluded. The " Pacifica " hypothesis would explain many plant distributions, both living and fossil. The possibility that it might account for marsupial and monotreme distribution cannot be excluded.

INTRODUCTION

In the last three years there have been several attempts to relate the biogeography of marsupials to plate tectonics but consensus seems to be limited to agreeing that the first topic is a real problem and its solution must somehow be sought in the second. Part of the diversity of opinion derives from the variety of geophysical reconstructions to which biogeographers can pin their ideas. However, there has also been important diversity of attitudes towards four biological topics, viz., the consideration given to mammals other than marsupials, the interpretation of the fossil record, chemical palaeogenetics, and the consideration given to similar distribution patterns among other organisms. Each of these four topics can throw light on the general problem and each will be discussed, but first the present distribution will be outlined.

2. — PRESENT DISTRIBUTION OF MARSUPIALS

Within America there are two major groups of marsupials, the didelphoids and caenolestoids, while in Australia — New Guinea there are three, the dasyuroids, perameloids and phalangeroids. The status of these groups will not be discussed now ; most accept the rank of super-family given by Simpson (1945). Most agree on the separateness of three of these groups but Brundin (1966), for example, disputes the separation at this level of the Australian dasyuroids and American didelphoids.

The caenolestoids are most abundant in the high Andes of north-western South America and probably occur in similar ecosystems at decreasing altitudes down to 43°S in Chile. The didelphoids are also most diverse in the north-west of South America but extend over all the continent except the southernmost 1500 km. They are well represented in Central America and *Didelphis* itself extends north into Canada.

All three Australian groups are widespread through the mainland, Tasmania and New Guinea. It is not always appreciated that the representation in New Guinea is very strong (Laurie and Hill, 1954). It is true that four of the ten extant Australian families are not found in New Guinea but all four are very small families (three are monospecific), specialised feeders, and the more extreme products of the well-known adaptive radiation into the many ecological niches of Australia. The six larger families are well represented in both islands and at least one of them (Peramelidae) attains its maximum diversity in New Guinea (Tate, 1948).

A few representatives have spread to islands near New Guinea but Keast (1968) convincingly suggests that man has been responsible. Apart from this, marsupials do not occur in neighbouring Indonesia or Melanesia, in New Zealand, or in any part of Africa or Eurasia.

3. — THE CONSIDERATION OF OTHER MAMMALS

The importance of considering other mammals when discussing marsupial biogeography derives from two ideas. The first is that important evolutionary events may have coincided with geographical separation and, therefore, the biogeography of related groups of similar rank must be taken into account. Hoffstetter (1970, 1972) suggested that the divergence of marsupials and placentals was associated

with an initial separation of Pangaea into America — Antarctica — Australia (marsupials) and Eurasia — Africa (placentals). Fooden (1972) also accepted the concept of Pangaea but suggested that the successive isolation by continental drift of Australia — New Guinea (180 m.y.b.p.) and South America (135 m.y.b.p.) left these continents with, respectively, prototherians plus marsupials and marsupials plus placentals. (The dates quoted are Fooden's).

Fooden's hypothesis will be criticised in a later section but, nevertheless, I believe he is right in considering prototherians at the same time as marsupials. Both groups survive in Australia — New Guinea and it seems probable that the same set of circumstances accounts for the presence of both ; at least, a single hypothesis which can account simultaneously for both is preferable to separate hypotheses for the two groups.

The three living genera of prototherians, all highly specialised feeders, are confined to Australia — New Guinea. The common echidna *(Tachyglossus)* is versatile and ranges over most of Australia as well as Tasmania and New Guinea. The other two genera are confined to the east, the platypus *(Ornithorhyncus)* not extending into New Guinea and *Zaglossus* only surviving in New Guinea (though there are late Tertiary fossils in Queensland). The fossil record of these monotremes is confined to the late Tertiary and adds nothing of biogeographical significance to what has already been said.

Until recently, the simultaneous consideration of monotremes placed no restrictions on hypotheses which accounted for marsupial biogeography ; having no significant fossil record and no living relatives outside Australia — New Guinea, any hypothesis which could account for the presence of marsupials could account for monotremes too. (However, it did weaken hypotheses which relied on low probability events, such as sweepstake dispersal). It now seems possible that this situation should be modified in the light of recent opinions (Kermack 1967, Hopson 1970) that other extinct primitive mammals should be grouped with the monotremes in the Prototheria. In particular, Kielan-Jawarowska (1970) and Kermack and Kielan-Jawarowska (1971) have given evidence that the monotremes are quite closely related to the extinct multituberculates. Thus it seems possible that the monotremes may now be removed from the old relict groups which have no close relatives (mentioned by Brundin in this symposium). If the multituberculates are indeed their sister group, then it is noteworthy that in Laurasia the multituberculates have a good fossil record but they have never been detected in a fragment of Gondwanaland (table 1). This suggests that the monotremes are derived from a Laurasian group and have never had the opportunity to spread far from where they are now found.

The second way in which the consideration of other mammalian groups is important derives from the idea that if geographical conditions had allowed the dispersal of one group, they should, in general, have allowed the dispersal of co-existing members of another group. Thus any hypothesis which allows the introduction of marsupials to Australia in the Tertiary from Asia or South America must account for the exclusion of the placentals which undoubtedly existed in these continents.

The most powerful hypothesis put forward in favour of marsupial dispersal from South America to Australia via Antarctica, that of Jardine and McKenzie (1972), can be seen to suffer in two respects, unless it is to fall back on low-probability events. First it is necessary to postulate that marsupials existed in SouthAmerica before placentals although there is no evidence for this. Second, it is necessary to have one hypothesis for marsupials and another for prototherians because there is no record of prototherians (e.g. multituberculates) ever having existed in South America. This discussion leads naturally into the next section.

4. — THE FOSSIL RECORD

a) *Summary of the information.*

The essential information about the distribution of fossils is given in Table 1. It should be noted that there is no record of marsupials from Asia, and Clemens (1968, 1970) has suggested that the sample of one late Cretaceous mammalian fauna from Mongolia is large enough to indicate that marsupials were not present. Nor are marsupials, either fossil or living, known from anywhere not included in the table.

TABLE 1. — Summary of distributions of fossils of multituberculates, monotremes, marsupials and placentals.

	Australia	South America	North America	Western Europe	Asia	Africa
Prototheria Multituberculates	—	—	Cretaceous Palaeocene Eocene	Cretaceous Palaeocene	Cretaceous Palaeocene Eocene	—
Monotremes	Pleistocene | Living	—	—	—	—	—
Marsupials	Oligocene | Living	Late Cretaceous | (Peru) Living	Late Cretaceous | Early Miocene [Extinct Period] Pliocene | Living	Eocene Early Miocene	—	—
Placentals (Excluding bats, seals etc.)	Late Tertiary | Living	Late Cretaceous | (Peru) Living	Late Cretaceous | Living	Palaeocene | Living	Late Cretaceous | Living	Oligocene | Living

Early and mid Cretaceous fossils of doubtful taxonomy have been omitted e.g. Holoclemensia (? marsupial), Pappotherium, Aegialodon, Endotherium (? placentals). It is not apparent that resolution of any of these doubts is crucial to the arguments presented in this paper.

Prototherian fossils, though not of multituberculates or monotremes, are known from the Jurassic (Cooke 1968) and Triassic (Crompton 1964) of Africa. With the exception of fossils from the upper Cretaceous of Peru (table 1) these are the only reliable Mesozoic mammalian fossils known from a remnant of Gondwanaland. [There are possible fossil mammalian footprints in South America (Casamiguela 1961). The report of Cretaceous mammalian fleas from Australia (Riek 1970) has been discounted by an eminent siphonapterologist (Smit 1972) and cannot be taken as serious evidence for the presence of mammals until properly substantiated].

b) *Interpreting the fossil record.*

Recent writers on marsupial biogeography appear to have widely divergent attitudes towards interpreting absences from the fossil record. Representing one extreme is Fooden (1972) whose hypothesis requires the presence of prototherians and marsupials in Australia from 180 m.y.b.p. although the earliest known fossils are about 30 m.y.b.p. He also requires prototherians and marsupials in South America since 135 m.y.b.p. although fossils of the former have never been found and the oldest marsupial fossils (Sige 1968) are late Cretaceous (the Cretaceous ended 65 m.y.b.p.). A similar attitude is displayed by Cox (1970) who would require the presence of marsupials in Australia from about 106 m.y.b.p. (Jardine and McKenzie 1972) and in Africa, where they have never been found, at about that time.

At the other extreme of interpretation are Jardine and McKenzie (1972) whose hypothesis takes close note of the absences of marsupials from the fossil record. Whereas the hypothesis of Fooden (1972) could be greatly strengthened by new discoveries, it could not be disproved by non-discovery. In most branches of science, a quantitative assessment of probability (P) would be made. In the absence of objective methods for doing this, individuals must assess subjectively and, while there will probably be agreement that the absence of marsupial fossils from a region like Antarctica cannot be regarded as significant, judgments will vary for inhabited and accessible lands. My own preference is for hypotheses which, like that of Jardine and McKenzie (1972), take account of absences from the fossil record and do least violence to them. For this reason, I reject the hypotheses of Fooden (1972) and of Cox (1970) but recognise that there is a subjective judgment involved.

c) *An interim interpretation of the fossil record.*

It follows from the last section that I favour the hypothesis that marsupials came to Australia from elsewhere, arriving no later than the Oligocene (about 30 m.y.b.p.). Other aspects of their evolution are, I believe, relatively non-controversial in comparison with the manner of their arrival in Australia. It is appropriate to discuss these less controversial aspects now as they do not depend on lines of evidence which have yet to be considered.

Clemens (1970, 1971), reviewing evidence from the fossil record, favoured the hypothesis that divergence of marsupial and placental lineages was an early Cretaceous event and that it probably coincided with geographical separation. Early diversification of placentals took place in what is now Eurasia and of marsupials in what is now North America. The fossil record of early marsupial evolution is confined to what is now the eastern margin of the Rocky Mountains but what was, in the late Cretaceous, the western shore of a sea connecting the present Gulf of Mexico and Arctic Ocean (Clemens 1970). In both western North America and Eurasia the earliest definite records, of marsupial and placentals respectively, are dated about 80 to 90 m.y.b.p. and multituberculates were present with both. While marsupials probably never appeared in Asia, placentals appeared in North America, though when is controversial. Clemens (1970) believed that " the first occurrence of placentals in North America might be pre-Campanian (i.e. before 76 m.y.b.p.), but that late Cretaceous North American placentals were an immigrant stock remains probable. " Subsequent to the arrival of comparatively advanced placentals in the Maestrichtian (72 to 65 m.y.b.p.), the marsupials declined (Lillegraven 1969) and eventually became extinct. Before they did so, however, the didelphid *Peratherium* spread through eastern North America and the appearance of this genus in western Europe in the Eocene is thought to have followed migration from North America (Clemens 1970). Studies of sea-floor

spreading (Avery et al. 1968, Phillips and Forsyth 1972) would allow interchange of faunas between Europe and North America vie Greenland until 65 m.y.b.p. when spreading along the Reykjanes ridge commenced. A land connection between Greenland and Britain was still present in the Eocene (Vogt 1972). Didelphoids became extinct in North America and Europe by the early Miocene. Different species of didelphoids from South America re-invaded North America when the present land connection was established in the upper Pliocene (Haffer 1970).

Until recently, marsupials had been known from South America only since the lower Palaeocene (Patterson and Pascual 1968) when didelphoids and caenolestoids were present together with five orders of placentals. Since four of these seven orders (Edentata, Condylarthra, Notoungulata and didelphoids) are known from the late Cretaceous of North America, they are presumed to have migrated from there. In 1967, Grambast et al. described from the Peruvian Andes the teeth of a condylarth, *Perutherium* (not to be confused with the didelphoid *Peratherium*) which, on the basis of contemporary spores of characean algae, they identified as upper Cretaceous. This age was later supported by reports of the presence of the egg-shells of dinosaurs and, in addition, the teeth of several species of didelphoid marsupials were detected (Sige 1968, 1971). Thus, although the entry of marsupials into South America has been put back to the upper Cretaceous, they are still accompanied by placentals.

It is usually assumed that the invasion of South America by mammals originated from North America. Recent reconstructions (Dietz and Holden 1970, Coney 1971, see also Haffer 1970) show a gap of about 2 000 km. between the south end of western North America and the north-west corner of South America at the end of the Cretaceous. How this was traversed by mammals is not clear. Eastward spreading of the Farallon plate from the predecessor of the East Pacific rise (Herron 1972) may have bridged the gap with an island arc (Moores 1970, Coney 1971) which is now represented by the Antilles and Venezuelan coast range.

It should be noted that important groups of mammals did not enter South America with the marsupials, edentates, condylarths and notoungulates. These include insectivores (s.l.), creodonts, carnivores, pro-simians and, of particular interest, multituberculates. For the placentals, this may possibly be explained by the timing of the two events, i.e. the presence of the bridge on the one hand and, on the other, the evolution or arrival in North America of different groups. The origin of the caenolestoids is unknown ; they were present in the earliest Palaeocene deposits of South America, radiated to attain considerable prominence and subsequently declined to their present obscurity. The third major group of American marsupials, the borhyaenoids, originated in South America and became extinct in the Miocene.

Although the above may contain some controversial points, it is believed that in broad outline it will be acceptable at present to many students. If it is accepted, then the main problem strips down to explaining the distribution of marsupials between the Americas (upper Cretaceous) and Australia-New Guinea (no later then the Oligocene). Having said this, the two remaining topics mentioned in the introduction can be discussed.

5. — "CHEMICAL PALAEOGENETICS"

This was the name given by Zuckerkandl (1965) to the study of evolution using the amino acid sequences of proteins. It is unfair to imply, as I did in the introduction, that there is diversity of attitudes to this topic because, in fact, it has not been discussed in relation to marsupial biogeography, the relevant data having been available only to the most recent authors. "Chemical palaeogenetics" allows the development of a phylogeny independent of classical methods and estimation of dates of divergence of taxa which, while not independent of the fossil record as a whole (e.g. of the mammals) can be independent of the fossil record of a particular group (e.g. of marsupials). Air, Thompson, et al (1971) have estimated the date of marsupial-placental divergence at 130 m.y.b.p. from the following data :

Protein	*Million years since divergence*	95 % *confidence limits*
Myoglobin	111	85-136
Haemoglobin α	139	123-154
Haemoglobin β	137	104-170

This date agrees well with the conclusion of Clemens (1970), mentioned in the previous section, that divergence was an early Cretaceous event.

The only other available date is that of Thompson and Air (1971) for the divergence of two subfamilies of kangaroos (the Macropodinae and Potoroinae) at 50 m.y.b.p. (with 95 % confidence limits 41-57 m.y.b.p.). The Australian marsupials are a relatively homogeneous group (Kirsch 1968) approximately equivalent to the didelphoids or caenolestoids as judged by serological techniques (Hayman et al, 1971). Before 50 m.y.b.p., the Australian marsupials must have separated from the American, the superfamily Phalangeroidea must have differentiated from the other two Australian superfamilies and the family Macropodidae must have differentiated from the remaining phalangeroid families.

Jardine and McKenzie have postulated a southern land-bridge from South America to Australia between 75 and 45 m.y.b.p. In view of the above observations it seems reasonable to suppose that this land bridge could only have been open in the early part of the period postulated, otherwise South America and Australia should share marsupial groups down to the sub-family level. The date also suggests either that there were marsupials in Australia before the time of the earliest fossils (about 30m.y. b.p.) or that marsupials evolved to sub-family level before they invaded the majority of what is now Australia — New Guinea.

6. — DISTRIBUTION PATTERNS AMONG OTHER ORGANISMS

a) *Introduction.*

The interchange of ideas between biogeography and plate tectonics should be two-way, though perhaps not equal. At present there is a desire to interpret biogeographical distributions in terms of the " hard facts " of geophysics. However, as one goes back in geological time, geophysical " facts " become softer until they are comparable with those of biogeography. I believe this to be the case now for the Mesozoic in the Pacific area. If geophysicists are to be induced to take as much notice of biogeography as biogeographers do of plate tectonics, they must be presented with distribution patterns, not explicable by modern dispersal and applying to a reasonably large and diverse range of organisms. This seeking after patterns is also, of course, beneficial to the biologist, because if a particular group (e.g. the marsupials) has a distribution pattern like many other organisms, one is more confident of its significance in terms of plate tectonics. The question then is, into what pattern, if any, do marsupials fit ?

TABLE 2. — *Amphi-Transpacific disjunct genera and higher taxa of angiosperms — from van Steenis (1962)*

	Number
North warm-temperate and sub-tropical	115
Tropical	80
South sub-tropical and warm-temperate	23
South Temperate	62

1. There are many north temperate and arctic cases but these are of no biogeographical significance in the present context.

2. " Temperate " includes not only lowlands at 45°-60° latitude but also altitudes of 2400-4000 metres in the equatorial zone ; thus a tropical distribution is not to be explained by a simultaneous altitudinal and northerly migration of a south temperate genus (e.g. up the Andes).

Clearly, the present distribution pattern of marsupials is amphi-transpacific in the terminology of van Steenis (1962) who recorded the number of cases of disjunct genera and higher taxa of angiosperms. His data are reproduced in Table 2. The two patterns most relevant to marsupials are tha south temperate and tropical ; each of these will be discussed and attempts made to fit marsupials into them.

h) *The South Temperate distribution pattern.*

This is, of course, the subject of one of the earliest and most durable generalisations of biogeography. In 1853, Sir Joseph Hooker listed 228 angiosperm species in a " Comparative table of plants which may be considered as representing one another (more or less remarkably) in two or all three south temperate land masses ", i.e. New Zealand, Australia and South America. Ha believed that he had discovered a botanical relationship " which is not be accounted for by any theory of transport or variation but which is agreeable to the hypothesis of all being members ol a once more extensive flora, which has been broken up by geological and climatic causes. " This conclusion has survived the immense literature it has invoked and has beea extended to organisms other than angiosperms.

Thc evidence, including that lor animals, was summarised by Darlington (1965) who has himself made an important generalisation. Thus (p. 107) " Most of the peculiar southern cold-temperate groups of plants and iuvertebrates that arc common to southern South America and southern Australia — Tasmania occur in New Zealand too ". This appears to be true ol the different groups of beetlcs which Darlington investigated himself. It is also true of the liverworts discussed by Schuster (1969) (whose remarks about the poor dispersal characteristics ol these organisms should be noted). Among the Diptera, the generalisstion holds quite well for at least two lamilics ; in the Mycetophilidae, out of 22 genera shared by southern South America and southeastern Australia, 15 are also lound in New Zealand (Freeman 1951) ; in thc Tipulidae the corresponding figures are 7 out of 11 ganera (Alexander 1929). Among the chironomid midges studied by Brundin (1966) (which will bc discussed again later) the generalisation holds for three large genera hut there are five small genera (3 to 7 species esch) not found in New Zealand.

This last example is tha chief exception to the generalisation ol which I am aware and it is possible that the explanation may be found in the following. Good (1964 appendix B) lists 28 genera (or sistar-pairs of genera) of angiosperms of which 7 are not found in New Zealand. Scrutiny shows that one of these *(Lomatia)* occurs in New Caledonia and two (*Eucryphia* and *Gevuina*) have sister-genera there (van Steanis and Balgooy 1966). New Caledonia is probably a northern outpost ol the same landmass that ineludes New Zealand (Fleming 1969). Thus Good's list of exceptions can be whittled down to even more insignificant proportions if Naw Zealand is extended to include New Caledonia. Perhaps some of Brundin's fiva excaptional genera (four ol which have members at low latitudes such as Peru or Queensland) might be similarly eliminated. I am unaware of any studies of the chironomids of New Caledonia.

While acknowledging that further assessment is desirable, at this stage I beliave Darlington's generalisation is a useful one. *Most* groups of plants and invertebrates shared by southern South America and south-east Australia *are* lound in Naw Zealand. This probably has a hasis in different land connections in the past. The relevant question is whether the explanation for thc exceptions, which some might hold to include marsupials, must ba sought in different land connections, or in extinction from New Zealand. It is my present belief that many of the exceptions to Darlington's generalisation might be accounted lor by " chance " extinction during tha last 80 m.y. Particular plant and invertebrate genera are likely to have escaped notice in tha fossil record.

Differential extinction may also account lor the situation found by Brundin (1966) in his thorough taxonomic studies of chironomid midges. These strongly suggest that, unlike New Zealand's, Australia's chironomids are highly specialised (apomorphic) relatives ol more generalised (plesiomorphie) types found in South America. They includa the five small genera already mantioned as being absent from New Zealand. While a simple explanation of this is that Australia's chironomids have been derived by migration from South America, it is not the only one. Both may have been derived

from a common area (the southern part of " South Pacifica " — see later) but conditions favouring extinction of chironomids may have been more prevalent in Australia so that only highly specialised types have survived there. Such conditions might well have occurred during the Cenozoic northerly drift of Australia.

It seems unlikely that extinction can account for the absence of marsupials from New Zealand, or non-discovery for their absence from the fossil record. This has been discussed by Flemming(1962)as follows : " ... it is difficult to suppose that mammals, once established, would have subsequently succumbed in a country that supported flightless rails and ratites until the dawn of the human period. Had dinosaurs (or early mammals) reached New Zealand by a land connection at the time *Nothofagus* came here, we would expect them to have survived as relics or to have radiated adaptively to fill some of the many empty niches in primitive New Zealand ".

To this must be added the fact that marsupials are only doubtful members of the south temperate fauna of South America; they do not occur in the southernmost 1500 km. of the continent. In summary, I believe that the weight of evidence is against marsupials belonging to the south temperate distribution pattern. The possibility cannot be excluded but there is sufficient reason to examine other distribution patterns.

c) *The tropical amphi-transpacific distribution pattern.*

Another quotation from Darlington (1965, p. 38) is : " South America and Australia do share some notable groups of vertebrates, including marsupials, leptodactylid and hylid frogs and chelyid turtles, but these are all mainly tropical or warm temperate animals. Most of them do not show special relationships between the southern cold-temperate forms on different continents ". If this opinion is correct, it focuses attention on the tropical amphi-transpacific distribution pattern.

The strongest support for the reality of such a pattern comes from the angiosperms and particularly from van Steenis (1962) who, as already noted (table 2), recorded 80 disjunct groups (of varying taxonomic ranks) confined to the tropics on both sides of the Pacific. In the same table he also recorded 81 similar tropical amphi-transatlantic groups, suggesting that the tropical floral connections across the two oceans are approximately equally strong. The figures given by Axelrod (1970) suggest that the transpacific link is weaker than the transatlantic ; at the family level his ratio was 8 to 12 while at the generic level it was 37 to 91. That about a quarter of the groups should be removed from the list of 80 recorded by van Steenis is indicated by a preliminary analysis of the data given by van Balgooy (1971) which suggests that about 20 groups are either not truly amphi-transpacific, or not truly tropical, or so widely spread in Pacific islands that their biogeographical significance must be doubted. Van Balgooy's survey was strictly confined to genera (not other taxonomic groups) ascertained by their presence in Pacific islands (not the adjoining continents) and thus offers no informations about many of van Steenis ' examples and is only capable of adding new examples at the generic level ; about 7 genera are in fact added. The overall impression from the three authors (van Steenis 1962, Axelrod 1970, van Balgooy 1971) is that, while not as strong as the transatlantic connection, the transpacific one is still strong. If we regard the former as a reflection of continental drift, we should take seriously the possibility that the tropical amphi-transpacific pattern might be explained similarly. That it is not due to over-land migration was concluded by Axelrod (1970) who reviewed the subject and stated, " The idea that taxa now common to the Old and New World tropical regions migrated from one area to the other via the North Atlantic and Beringia during Paleogene times finds no support from paleobotanic or paleoclimatic evidence, and is also inconsistent with their adaptive and evolutionary relations. "

Can marsupials be related to such a pattern ? If Darlington's opinion that they are of tropical origin is correct, they may be. However, the present distributions of tropical transpacific plant groups on the western side of the Pacific ocean often include areas where marsupials do not occur, such as Indonesia, China and even Japan (see also Mackawa 1965). The majority of amphi-transpacific plant distributions include New Guinea and/or Queensland and it is conceivable that some tropical plants, but not marsupials, may have been able to migrate from these areas. Thus the idea that the angiosperm and marsupial distributions are connected need not be dismissed although the connection is rather loose and needs more detailed investigation.

7. — ASSESSMENT OF HYPOTHESES ABOUT MARSUPIAL BIOGEOGRAPHY

With the above ideas in mind we can now discuss the three main hypotheses about marsupial biogeography.

a) *Northern dispersal.*

Dispersal from North America to Australia via Asia can be dismissed briefly. Australia and East Antarctica separated in the Eocene (Le Pichon 1968, Sproll and Dietz 1969). The date favoured by Jardine and McKenzie (1972) is 43 m.y.b.p. although palaeontologiste record the first marine incursion south of Australia at about 48 m.y.b.p. (Mc Gowran 1971). Since then Australia has moved north by between 30° and 15° of latitude depending on whether or not the ridge also migrated. This appears to rule out any contact with Asia before the Oligocene. If, despite their absence from Indonesia or Asia both now and in the fossil record, marsupials had entered from the north when Australia eventually collided, it is most unlikely that they would not have been accompanied by placentals which were undoubtedly well-established in Asia by that time. I have expreesed this opinion before (Martin 1970) and see no reason to change it. Cox (1970) has also argued convincingly against the hypotheeis.

b) *Southern dispersal.*

Dispersal of marsupials to Australia from South America via Antarctica is an hypothesis that has been advanced by many authors but attention will be directed to the paper of the latest and strongest champions, Jardine and McKenzie (1972). The basis of their paper was laid in geophysical reconstructions by McKenzie and Sclater (1971) of the Indian ocean for 36, 45 and 75 m.y.b.p. Although their detailed studies did not extend to the South Pacific, their reconstructions revealed a land bridge from South America to West Antarctica to East Antarctica and Australia and this was an obvious route for marsupial dipersal. The biogeographical objections will be summarised shortly but first there is one geophysical objection, viz. that the geography of West Antarctica may have been oversimplified. If all the ice were removed from West Antarctica now, an archipelago would be revealed which, even allowing for the resultant uprising, would not form a land bridge like the one Jardine and McKenzie (1972) have invoked (Anderson 1965, Hamilton 1967, Schopf 1970). Palaeomagnetic pole determinations (Scharon et al. 1970, Blundell 1962) indicate that two parts of West Antarctica have had separate histories in the Mesozoic. The Antarctic peninsular has a Cretaceous pole close to the present one and may indeed have moved little since then. However, a Cretaceous pole from Marie Byrd Land is at 105°E., 30°S. and strongly indicates a separate movement from a location to the north in the Pacific Ocean. Scharon et al (1970) suggest that Antarctica should be thought of as three separate parts — the Antarctic peninsular, West Antarctica and East Antarctica. These points are illustrated in figure 1.

No Cretaceous pole is known for East Antarctica so that the palaeomagnetic test of McKenzie and Sclater's (1971) 75 m.y.b.p. reconstruction (their Table 11 and Figure 46) depends, as far as Antarctica is concerned, on the pole for the Antarctic peninsular alone. The Jurassic pole for East Antarctica (Beck 1972) is about 80° of arc away from the reported Jurassic pole for the Antarctic peninsular (see Creer 1970, p. 391 for discussion). Nevertheless, it is conceivable that by 75 m.y.b.p. East Antarctica and the Antarctic peninsular, but not West Antarctica, could have arrived in the positions shown by McKenzie and Sclater (1971) and there might have been a land bridge from the root of the Antarctic peninsular to East Antarctica (Anderson 1965 pp. 52-53) despite the absence of West Antarctica.

Thus Jardine and McKenzie's (1972) general hypothesis cannot be dismissed on geophysical grounds though I believe these grounds should remain in question until a study, complementary to that of McKenzie and Sclater (1971) of the Indian ocean, has been completed for the South Pacific and South Atlantic. Factors such as the above and the following should be assessed properly. The Endeavour fracture zone (Fig. 1) has been reliably plotted north of the Pacific — Antarctic ridge (Christoffel and Ross 1970). It finishes adjacent to the New Zealand platform at the anomaly corres-

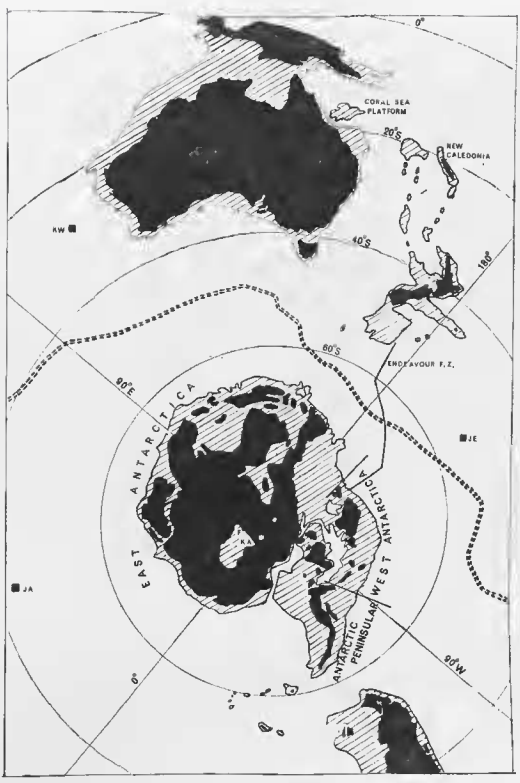

FIG. 1. — Map centred on Antarctica. Black above sea-level, hatched sea-level to -1000 metres. Antarctic contours according to Schopf 1970 ; note depths within West Antarctica of more than 1000 metres (down to 2500 metres). According to Anderson (1965) and Hamilton (1967), West Antarctica would be an archipelago even after rising following removal of ice. Division between West Antarctica and Antarctic Peninsula according to Scharon et al (1970). Approximate position of South-east Indian-Pacific Antarctic ridge shown in double dashed lines. Endeavour fracture zone north of ridge after Christoffel and Ross (1970) ; it has been extrapolated south of ridge. Former virtual geographic poles shown in squares ; KW Cretaceous West Antarctica, KA Cretaceous Antarctic peninsular, JA Jurassic Antarctic peninsular, JE Jurassic East Antarctica. P is south pole.

ponding to 80 m.y.b.p. If it is extrapolated to the south it finishes adjacent to the continental platform of West Antarctica near the Edsel Ford Ranges of Marie Byrd Land. It may reasonably be assumed that the two land masses were joined before 80 m.y.b.p. (Scharon et al 1970). If one takes notice of the Cretaceous pole for Marie Byrd Land, this continent, which I shall refer to as " South Pacifica ", was positioned well to the north in the Pacific ocean and, *contra* most reconstructions, much nearer the South American margin of Gondwanaland than the Australian one.

While discussing the reconstructions of McKenzie and Sclater (1971), it is profitable to point out another implication, though this is not necessarily an adverse criticism. They state " the accuracy of the latitude of a point on a plate in the reconstructions is less accurate than the relative positions of two points on different plates ". Nevertheless, the 75 m.y.b.p. reconstruction was tested against palaeomagnetic pole positions ; in it South America and Africa appear about 2° south of present latitudes. The 45 m.y.b.p. reconstruction was not so tested and, in view of the quotation above, it is not valid to take literally the fact that, in their figure 44, Africa and South America are shown about 14° of latitude further south than in the 75 m.y.b.p. reconstruction. If one assumes that this " 14° bob " is an artefact and move Africa and South America to their present latitudes, this has the effect of placing Australia nearer the south pole so that the juncture with East Antarctica is near the Antarctic circle, as it is also in their 75 m.y.b.p. reconstruction. This is illustrated in figure 2. One implication is that, since 45 m.y.b.p., eastern Australia has moved at least 30° north (the ridge having moved at least 15° north). This is not supported by the most relevant palaeomagnetic pole position which indicates that since 51.6 m.y.b.p. Australia has moved north by 17°, this figure being based on a pole position with 95 % confidence limits of radius 5.3.° (Wellman et al. 1969). A second implication concerns the climate and vegetation. There is good evidence (McGowran 1971) for warm water (though not tropical) in the upper Eocene off southern Australia. A land flora dated just prior to separation (49 m.y.b.p.) and from close to the site of separation (see figure 2) has been studied (Lange 1970, Southcott and Lange 1971). The fossils from this Maslin flora resemble the forest floor litter from present-day sub-tropical Queensland. While it may be conceivable that temperatures could be compatible with this, day-length must also be considered and it seems surprising that such a flora could have existed near the Antarctic circle. Either this anomaly, or the " 14° bob ", requires an explanation.

The biological arguments against southern dispersal in the period between 75 m.y.b.p. and 45 m.y.b.p. are :

a) One hypothesis is needed for marsupials and another for prototherians.

b) At least in the later stages, Australian marsupial sub-families had evolved and their exclusion from South America must be accounted for.

c) Placentals were present in South America at the same time as marsupials and their exclusion from Australia must be accounted for.

d) If a southern land bridge existed between 75 and 45 m.y.b.p. there should be biogeographical links between southern South America and south-east Australia. There are, but most components of this South Temperate biota, unlike marsupials, are also found in New Zealand. New Zealand's last episode of drifting having begun at 80 m.y.b.p., the implication is that the South Temperate biota originated before 80 m.y.b.p. and did not include marsupials.

There seem to be at least two possible solutions. Both start with " South Pacifica " isolated in the Pacific until 80 m.y.b.p. This accords with the conclusions of Fleming (1962, 1969) that, except in the upper Jurassic and lower Cretaceous when many Tethyan immigrants arrived, New Zealand had been isolated and, since then, has received only a trickle of immigrants by long range dispersal. From the lower Cretaceous until 80 m.y.b.p., the biota would have evolved and, it is proposed, is the ancestral source of the present South Temperate biota. At 80 m.y.b.p. the Pacific-Antarctic rise divided " South Pacifica ", moving the New Zealand platform to its present position. From this point there are two possibilities. First, to the south, islands were separated and, on the eastern side these carried the South Temperate biota to southern Chile. On the western side Marie Byrd Land collided with East Antarctica south of Tasmania's position at that time. On this hypothesis there has never been a land-bridge between South America and Australia. Marsupials did not disperse

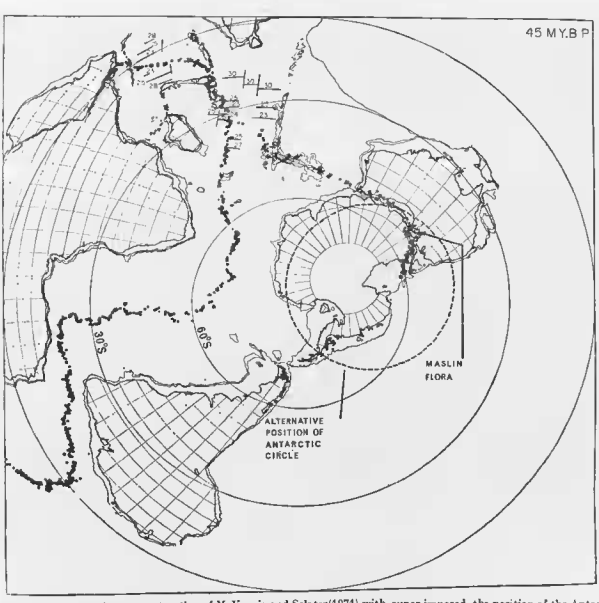

FIG. 2. — The 45 m.y.b.p. reconstruction of McKenzie and Sclater(1971) with, super-imposed, the position of the Antarctic circle if the pole is moved so that Africa and South America are in the latitudes which they occupy now and in the 75 m.y.b.p. reconstruction of the same authors. The position of the sub-tropical Maslin flora (49 m.y.b.p.) is also marked. Note (1) McKenzie and Sclater (1971) did not test this 45 m.y.b.p. reconstruction against the pole position as stringently as they did their 75 m.y.b.p. reconstruction. (2) The relative positions of South America, Antarctica and Australia are nearly the same in the 45 and 75 m.y.b.p. reconstructions. (3) This figure is identical with figure 3 of Jardine and McKenzie (1972) (except for my two additions).

this way. Brundin's pattern of chironomid relationships derives from the idea that the islands going to both South America and Australia were from the southern part of "South Pacifica" and there has been a more severe pattern of extinction in Australia.

The second solution is that the southern part of "South Pacifica" collided with both southern South America and East Antarctica thus forming a land bridge. It must have existed at about the end of the Cretaceous and could not have persisted for very long. Across this there could have been one-way dispersal of marsupials (but not placentals) and chironomids but, on the evidence of Darlington's generalisation, not very much more. A separate hypothesis is needed to account for the pre-

sence of prototharians in Australia — New Guinea. Three propositions must be invoked to account for the non-migration eastwards of the very characteristic part of the Australian flora so notably absent from South America (and New Zealand). First, this flora evolved in the western half of Australia ; second, this must have been separated from the eastern half by a barrier to migration ; third, this barrier must have extended south into East Antarctica.

My own assessment is that, while this second possibility cannot be discounted, the probability that marsupials having been dispersed by a southern route is low enough to justify serious consideration of other hypotheses.

c) *Trans-Pacific dispersal.*

Three years ago I briefly reviewed the northern and southern dispersal route hypotheses for marsupials (Martin 1970), found them as doubtful as I do today, and suggested that their weaknesses justified consideration of dispersal across the Pacific by division of a hypothetical land mass. " Pacifica " is an old idea which dates back to Hallier (1912) who invoked it as the birthplace of the angiosperms (see Takhtajan 1969 for a brief discussion). Such an hypothesis, if it had a geophysical basis, would be an answer to four important and related phytogeographical problems. The first has already been mentioned, viz. the many modern disjunct transpacific plant distributions. The second is the disjunct trans-pacific fossil plant distributions such as the Carboniferous *Gigantopteris* flora (Seward 1931) and the Mesozoic Cycadeoidea (Krassilov 1972). The third is the growing consensus of opinion, based on present distributions of plant families considered to be primitive, that the angiosperms originated in lands at present around the borders of the Pacific ocean (see particularly Takhtajan 1969 and Smith 1970). The fourth is the evidence for a Mesozoic north-south migration route in the Pacific (Melville 1966, 1967, 1969) which accounts for the hour-glass-shaped bi-hemispheric distributions such as that of the Fagoideae (*Nothofagus* and *Fagus*) (van Steenis 1971).

These problems were considered by Melville (1966, 1967, 1969) who has grasped the nettle and named those present lands which he thought might have formed parts of a Mesozoic " Pacifica ", probably with northern and southern components only temporarily connected. The concept does not seem to have been seriously discussed by zoogeographers though Krassilov (1972) has implied that it could account for the distribution of horned dinosaurs (ceratopsians), between Mongolia and western North America, which was described by Colbert (1948). Wilson (1968) has drawn attention to the distributions of earthworms of the genus *Plutellus* (Omodeo 1963) and land gastropods of the family Camaenidae (Walden 1963). In this symposium there have been discussions about at least three more animal groups which may be good examples of amphi-transpacific distributions, viz. leptodactylid and hylid frogs (Cracraft) and osteoglossomorph fish (Patterson). The idea should have some interest for those biologists who agree with Clemens (1970) that the evolutions of angiosperms, insects and primitive mammals were intimately linked.

The geophysical basis invoked by both Melville (1966) and myself (Martin 1970) to account for the spread was the Darwin rise (Menard 1964, 1969). The Darwin rise has faded into obscurity following the successes of the hypotheses of sea-floor spreading and plate tectonics. These have led to the realisation that much of the present Pacific ocean had been occupied in the Mesozoic by the Kula and Farallon plates, both now largely sub-ducted (Atwater 1970). Even if the former existence of the Darwin rise is doubtful in the form that Menard postulated, nevertheless the idea of a north-westerly trending Mesozoic rise in the Pacific is still very much alive. Until 10 m.y.b.p. such a rise was active as the border between the Pacific and old Farallon plates (Herron 1972). Much of the Pacific plate must have been formed by its activity. Since no part of the Pacific floor is older than Jurassic (136-190 m.y.b.p.) it follows that, theoretically at least, land separated on a ridge during the Jurassic could have spread to opposite margins since then.

Menard (1964) suggested that there could have been continental movement in the Mesozoic Pacific associated with the Darwin rise. Whether this was possible in relation to more recent ideas is unknown but it cannot be dismissed. McElhinny (1971) analysed palaeomagnetic pole positions and, because pole paths only converge with that of Siberia in the Cretaceous, suggested that " the

Verkhoyansk (eastern Siberia) and Sikhote Alin (east of Manchuria) regions were separate continental fragments which have been welded onto Asia leaving behind the Pacific ocean as seen today." Presumably this movement was associated with the Kula plate. (The implications for biogeographers interested in Mesozoic Beringia are important). There is now a great deal of evidence that parts of the west coast of North America have polar wandering curves which suggest that they originated to the south and west of the main part of the continent which they joined in the Cretaceous (Beck and Noson 1972, Packer and Stone 1972; see also Saad 1969 and Ernst 1970). Wilson (1968) suggested that parts of other continents from the west were driven against and under North America causing the uplift in Nevada and Alberta; Wilson and Burke (1972) have re-affirmed this. Islands of the size discussed by Wilson could have had profound biogeographical consequences.

On the western side of the Pacific the situation is much more complex due, among other things, to the existence of extensive marginal basins (Karig 1971). I have speculated (Martin 1970) that part of New Guinea (i.e. the Coral Sea Zone of Glaessner 1950) and/or the Coral Sea Platform (often called the "Queensland plateau" but I prefer the name proposed by Fairbridge 1950) might have spread from the Darwin rise carrying marsupials and, I would now add, monotremes; when Australia moved north in the mid-Tertiary, it collided with these former islands and their biota gained access to the mainland. I still believe this remains a possibility that cannot be dismissed. In order to spread westward from the rise between the Pacific and Farallon plates to the longitude of eastern Australia, rapid rates of plate movement may have been required. Such rapid rates are known from other parts of the world; e.g. 7-9 cms. per year for simple spreading (Larson and Chase 1970), 16-18 cms. per year under the concurrent influence of two spreading ridges (Herron 1972), and 11 cms. per year for the Turkish plate due to the scissor-like action of the Eurasian and Arabian plates (McKenzie 1970).

Trans-Pacific dispersal of marsupials has been criticised on two grounds. First, it has been said to be unrealistic and at complete variance with current data and concepts of continental movement (Cox 1970, Keast 1971). I cannot accept this, especially in view of our present ignorance about tectonic events in the western Pacific in the Mesozoic. The other criticism (Cox 1970) is that it does not explain how marsupials arrived in the hypothetical Pacific land-mass. While I believe that it is premature to either ask or answer that question, I would point out that they did not necessarily migrate there in marsupials form; for example, the separation of marsupial and placental lineages could have coincided with the separation of the hypothetical Pacific land-mass from part of present Eurasia.

My present belief is that it is too early to assess the hypothesis of trans-Pacific dispersal of marsupials. Southern dispersal via Antarctica may yet prove to be reasonable but it now presents sufficient difficulties to rate as low the probability of this hypothesis being correct. This is a good reason for retaining an open mind about trans-Pacific dispersal.

8. POSTSCRIPT — NEW GEOPHYSICAL EVIDENCE

New geophysical papers encourage me to re-emphasise my conclusion that it is too early to assess many problems of Pacific biogeography in the light of plate tectonics. Outstanding papers of great relevance are those of Larson and Chase (1972) and Larson and Pitman (1972) who take a step further in elucidating the ridge system separating the Pacific, Kula, Farallon and Phœnix plates during the Mesozoic (figure 3). The rapidity of movement is illustrated by Larson and Pitman's estimations that at 100 m.y.b.p. the rate of spreading between the Pacific and Farallon plates was 10 cms. per year while between the Pacific and Phoenix plates it was as fast as 18 cms. per year. The magnitude of the events can be gauged from their estimations that, since the Cretaceous, at least 7000 kms, of oceanic lithosphere have been underthrust beneath North America, a similar amount beneath Eurasia and about 5 000 kms. beneath South America and/or western Antaretica. The possible movement of land associated with these events has not been discussed and neither has the effect on lands and marginal seas of the western Pacific. Other new papers relevant to this last area have been published. Although largely concerned with establishing a principle, Fitch (1972) has thrown some light on the complex area between China and Australia and has recognised the China plate (which he

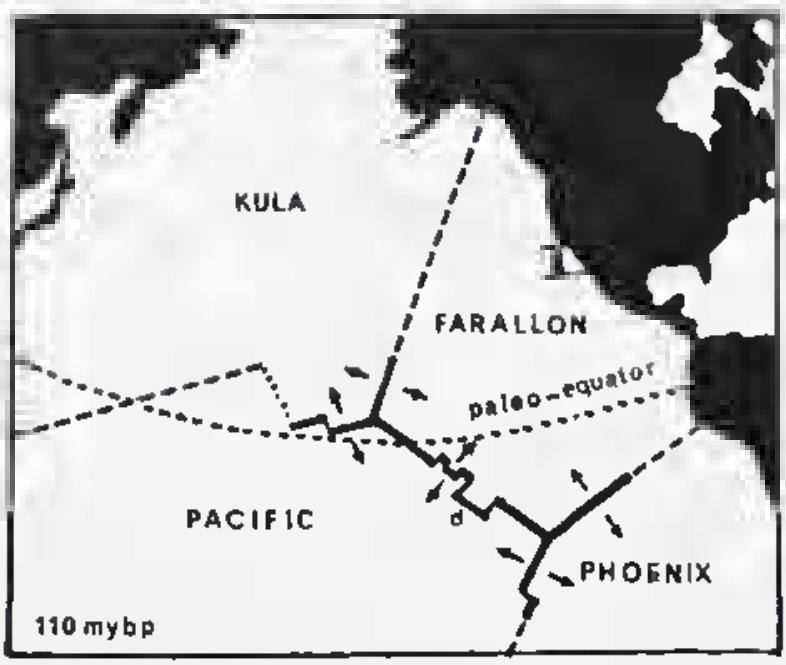

FIG. 3. — Map re-drawn from Larson and Pitman (1972) showing the Pacific, Kula, Farallon and Phœnix plates at 110 m.y.b.p. The ridges separating the plates are plotted relative to the Atlantic Ocean continents at that time and the plot construction is based on the present-day location of North America so that the paleo-equator appears as a curved line. Probable extensions of ridges are shown as dashed lines. The Kula plate is now entirely subducted. The ridge between the Farallon and Pacific plates is now extinct and part is subducted beneath North America; to illustrate its movement, the fracture zones bounding the prominent displacement (d) in it are shown in their present positions relative to the adjacent coast of California with, at right angles and nearly north-south, the magnetic lineation corresponding to about 30 m.y.p.b. For clarification of the southern triple junction, see Herron (1972).

shows as including the Sikhote Alin region mentioned earlier) as having been distinct from the Eurasian plate. The Indonesian area has also been considered by Audley-Charles et al. (1972) who discuss the events consequent upon Australia's northerly movement in the Tertiary. It is interesting that, like Rod (1966), these authors have been influence by du Toit (1937) through Carey (1958) to place central New Guinea north-east of Australia and rotating anti-clockwise into its present position. It is particularly interesting that Johnson and Molnar (1972) have been led to conclude that during its northerly drift, Australia (including southern New Guinea) collided with an island arc, the " Papuan arc ", which is now part of New Guinea ; this arc might well correspond with the marsupial-bearing islands I have formerly postulated (Martin 1970).

While believing that it is premature to suggest particular solutions, I nevertheless think that there are some indications about what will be important in deriving those solutions. The riddle of the origins of the flora and fauna of New Zealand, including the explanation for the South Temperate biota, will, I believe, be solved when the connection is established between the tectonic events associated with the system of ridges described by Larson and Chase (1972), Larson and Pitman (1972) and Herron (1972) and the geological and biogeographical histories of New Zealand as they have been described by Fleming (1969). I believe the solution may be compatible with the suggestion I have already made above. If this does not also solve the problem of marsupial distribution, and I have already given reasons why I think this is improbable though possible, then the next focus of attention should be New Guinea. If part of New Guinea was indeed formerly north-east of Australia and oriented north-westerly, then it is possible that it was derived from the parallel Pacific-Farallon ridge. It is worth repeating the statement of Rod (1966) that " the major late Cretaceous and especially

Tertiary faults of New Guinea are the expression of a tremendous drag towards the west combined with a small anti-clockwise rotation ". That central New Guinea may not have been as closely applied to Australia as Audley-Charles et al.(1972)indicate, is strongly suggested by the marked difference between the two floras (Good 1961, van Balgooy 1971) despite the fact that southern New Guinea is tectonically part of Australia (Glaessner 1950, Audley-Charles et al. 1972). The causes of central New Guinea's postulated movements, and of the great westward salient of the Pacific plate north of New Guinea, are clearly of the greatest interest.

REFERENCES

Air, G. M., Thompson, E. O. P., Richardson, B. J., Sharman, G. B. — Amino-acid sequences of kangaroo myoglobin and haemoglobin and the date of marsupial-eutherian divergence. Nature **229**, 391-394 (1971)

Alexander, C. P. — Diptera of Patagonia and South Chile I. Crane-flies. British Museum (Natural History) publication (1929).

Anderson, J. J. — Bedrock geology of Antarctica : a summary of exploration 1831-1962. Am. Geophys. Union, Antarctic Res. Ser. **6**, 1-70 (1965).

Atwater, T. — Implications of plate tectonics for the Cenozoic tectonic evolution of western North America. Geol. Soc. America Bull. **81**, 3513-3536 (1970).

Audley-Charles, M. G., Carter, D. J., Milsom, J. S. — Tectonic development of Eastern Indonesia in relation to Gondwanaland dispersal. Nature Phys. Sci. **239**, 35-39 (1972).

Avery, O. E., Burton, G. D., Heirtzler, J. R. — An aeromagnetic survey of the Norwegian Sea. Journ. Geophys. Research **73**, 4583 (1968)

Axelrod, D. I. — Mesozoic paleogeography and early angiosperm history. Bot. Rev. **36**, 277-319 (1970).

Beck M. E. — Palaeomagnetism and magnetic polarity zones in the Jurassic Dufek intrusion, Pensacola mountains, Antarctica. Geophys. J. R. astr. Soc. **28**, 49-63 (1972).

Beck, M. E., Noson, L. — Anomalous palaeolatitudes in Cretaceous granitic rocks. Nature Phys. Sci. **235**, 11-13 (1972).

Blundell, D. J. — Palaeomagnetic investigations in the Falkland Islands dependencies. Brit. Antarctic Surv. Sci. Rept. **39**, 1-24 (1962).

Brundin, L. — Transantarctic relationships and their significance, as evidenced by chironomid midges with a monograph of the subfamilies Podonominae and Aphroteniinae and the austral Heptagyiae. Kungl. Svenska Vetensk. Handl. **11**, 1-472 (1966).

Carey, S. W. — In " Continental drift. A symposium " (edited by S.W. Carey), 177. (Univ. of Tasmania, Hobart) (1958).

Casamiquela, R. M. — Sobre la presencia de un mammifero en el primer elenco (lenologica) de vertebrados del Jurassico de la Patagonia. Physis **22**, 225-233 (1961).

Christoffel, D. A., Ross, D. I. — A fracture zone in the southwest Pacific basin south of New Zealand and its implications for sea floor spreading. Earth and Planetary Sci. Letters **8**, 125-130 (1970).

Clemens, W. A. — Origin and early evolution of marsupials. Evolution **22**, 1-18 (1968).

Clemens, W. A. — Mesozoic Mammalian Evolution. Annual Rev. Ecology and Systematics **1**, 357-390 (1970).

Clemens, W. A. — Mammalian evolution in the Cretaceous. In " Early mammals" (edited by D.M. and K.A. Kermack. Supplement nº **1** to Zool. J. of Linn. Soc. Vol. 50) Academic Press (London) (1971).

Colbert, E. H. — Evolution of the horned dinosaurs. Evolution **2**, 145-163 (1948).

Coney, P. J. — Cordilleran tectonic transitions and motion of the North American plate. Nature **233**, 462-465 (1971).

Cooke, H. B. S. — The fossil mammal fauna of Africa. Quart. Rev. Biol **43**, 234-264 (1968).

Cox, C. B. — Migrating Marsupials and drifting continents. Nature **226**, 767-770 (1970).

Creer, K. M. — A review of palaeomagnetism. Earth-Science Reviews **6**, 369-466 (1970).

Crompton, A. W. — A preliminary description of a new mammal from the Upper Triassic of South Africa. Proc. Zool. Soc. London **142**, 441-452 (1964).

Darlington, P. J. — Biogeography of the Southern End of the World. Harvard University Press (Cambridge, Massachusetts) (1965).

Dietz, R. S., Holden, J. C. — Reconstruction of Pangaea ; breakup and dispersion of continents, Permian to present. Journ. Geophys. Research **75**, 4939-4956 (1970).

Du Toit, A. L. — " Our wandering continents : an hypothesis of continantal drift. " (Oliver and Boyd, Edinburgh) (1937).

Ernst, W. G. — Tectonic contact between the Franciscan melange and the Great Valley sequence — crustal expression of a late Mesozoic Benioff zone. Journ. Geophys. Research **75**, 886-901 (1970).

Fairbridge, R. W. — Recent and pleistocene coral reefs of Australia. J. Geology **58**, 330-441 (1950).

Fitch, T. J. — Plate convergence, transcurrent faults, and internal deformation adjacent to south-east Asia and the Western Pacific. Journ. Geophys. Research **77**, 4432-4460 (1972).

Fleming, C. A. — New Zealand biogeography — a palaeontologist's approach. Tuatara **10**, 53-108 (1962).

Fleming, C. A. — The Mesozoic of New Zealand; chapters in the history of the circum-Pacific mobile belt. Q. Jl. geol. Soc. Lond. **125**, 125-170 (1969).

Fooden, J. — Breakup of Pangaea and isolation of relict mammels in Australia, South America, and Madagascar. Science **175**, 894-898 (1972).

Freeman, P. — Diptera of Patagonia and South Chile 111 Mycetophilidae British Museum (Natural History) publication (1951).

Glaessner, M. — Geotectonic position of New Guinea. Amer. Assoc. Petrol. Geol. **34**, 856-881 (1950).

Good, R. — The geography of flowering plants, 3 rd ed. Longmans, London (1964).

Gambast, L., Martinez, M., Mattauer, M., Trales, L. — *Perutherium altiplanensa* Nov. Gen., nov. sp., premier mammifère Mesozoïque d'Amérique du sud. Comptes Rend. Acad. Sci (Paris) **264**, 707-710 (1967).

Happer, J., — Geologic-climetic history and zoogeographic significance of the Urabs region in north-western Colombia. Caldasia **10**, 602-636 (1970).

Hallier, H. — Über frühere landbrücken pflanzen und wolkerwanderungen zwischen Australien und Amerika. Med. Rijksherb., Leiden **13**, 1-32 (1912).

Hamilton, W. — Tectonics of Antarctica. Tectonophysics **4**, 555-568 (1967).

Hayman, D. L., Kirsch, J. A. W., Martin, P. G., Waller, P. F. — Chromosomal and serological studies of the Caenolestidae and their implications for marsupial evolution. Nature **231**, 194-195 (1971).

Herron, E. M., — Sea floor spreading and the Cenozoic History of the east-central Pacific. Geol. Soc. Amer. Bull. **83**, 1671-1692 (1972).

Hoffstetter, M. R. — L'histoire biogeographique des marsupiaux et la dichotomie marsupiaux-placentaires. Comptes Rend. Acad. Sci. (Paris) **271**, 388-391 (1970).

Hoffstetter, M.R. — Données et hypothèses concarnant l'origine et l'histoire biogéographique des Marsupiaux C. R. Ac. Sc. (Paris) **274**, 2635-2638 (1972).

Hooker, J. D. — The Botany of the Antaretic voyage of H. M. discovery shipsErebus and Terror in the years 1839-1843. II. Flora Novae-Zelandiae. Part 1. Flowering plants. Introductory essay. Lovell Reeve (London) (1853).

Hopson, J. A. — The classification of non-therian mammals. J. Mammalogy **51**, 1-9 (1970).

Jarmine, N. and D. McKenzie — Continental Drift and the dispersal and evolution of organisms. Nature **235**, 20-24 (1972).

Johnson, T. and Molnar, P. —Focal mechanisms and plate tectonics of the southwest Pacific. Journ. Geophys Research **77**, 5000-5032 (1972).

Kasig, D. E. — Origin and davalopment of marginal basins in the western Pacific. Jour. Geophys. Research **76**, 2542-2561 (1971).

Keast, A. — Australian mammals : zoogeography and evolution. Quart. Rev. Biol **43**, 373-408 (1968).

Keast, A. — Continental drift and the evolution of biota on southern continants. Quart. Rev. Biol. **46**, 335-378 (1971).

Kermack, K. A. — The interrelations of early mammals. J. Linn. Soc. (Zool.) **47**, 241-249 (1967).

KERMACK, K. A. and KIELAN-JAWOROWSKA, Z. — Therian and non-therian mammals. In "Early Mammals" (edited by D. M. and K. A. KERMACK. Supplement nº 1 to Zool. J. of Linn. Soc. Vol. 50, Academic Press (London) (1971).

KIELAN-JAWAROWSKA, Z. — Unknown structures in multituberculate skull. Nature **226**, 974-976 (1970).

KIRSCH, J. W. A. — Prodromus of the comparative serology of Marsupialia. Nature **217**, 418-420 (1968).

KRASSILOV, V. A. — Phytogeographical classification of Mesozoic floras and their bearing on continental drift. Nature **237**, 49-50 (1972).

LANGE, R. T. — The Maslin Bay flora, South Australia. N. Jb. Geol. Palaont. Mh. **8**, 486-490 (1970).

LARSON, R. L., CHASE, C. G. — Relative velocities of the Pacific, North America and Cocos Plates in the middle America region. Earth and Planetary Sci. Letters **7**, 425-428 (1970).

LARSON, R. L., CHASE, C. G. — Late Mesozoic evolution of the western Pacific. Geol. Soc. America Bull. **83**, 36 273644 (1972).

LARSON, R. L., PITMAN, W. C. — World-wide correlation of Mesozoic magnetic anomalies and its implications. Geol. Soc. America Bull. **83**, 3645-3662 (1972).

LAURIE, E. M. O. and J. E. HILL. — List of land mammals of New Guinea, Celebes and adjacent Islands, 1758-1952. British Museum (Natural History) publication (1954).

LE PICHON, X. — Sea floor spreading and continental drift. Jour. Geophys. Research **73**, 3661-3697 (1968).

MCELHINNY, M. W. — Palaeomagnetism and plate tectonics of eastern Asia (abstract only). Proceedings 12th Pacific Science Congress, Canberra (1971).

MCGOWRAN, B. — Australia-Antarctica separation and the Eocene transgression in southern Australia. South Australian Department of Mines unpublished report 71/78 (1971).

MCKENZIE, D. P. — Plate tectonics of the Mediterranean Region. Nature **226**, 239-343 (1970).

MCKENZIE, D., SCLATER, J. G. — The evolution of the Indian Ocean since the late Cretaceous. Geophys. J. R. astr. Soc. **25**, 437-528 (1971).

MAEKAWA, F. — Floristic relation of the Andes to eastern Asia with special reference to the trans-palaeo-equatorial distribution. Journ. Fac. Sci. Univ. Tokyo **fff, 9**, 161-195 (1965).

MARTIN, P. G. — The Darwin Rise hypothesis of the biogeograpbical dispersal of marsupials. Nature **225**, 197-198 (1970).

MELVILLE, R. — Continental drift, mesozoic continents and the migrations of the angiosperms. Nature **211**, 116-120 (1966).

MELVILLE, R., — The distribution of land around the Tethys sea and its bearing on modern plant distribution Systematics Association publication No. 7 (Aspects of Tethyan biogeography — Eds. C. G. Adams and D. V. Ager) 291-312 (1967).

MELVILLE, R. — Phil. Trans. Roy. Soc. B **255**, 617-620. (no title).

MENARD, H. W. — Marine geology of the Pacific. Mc Graw Hill Book Co., New York (1964).

MENARD, H. W. — Growth of drifting volcanoes. Jour. Geophys. Research **74**, 4827-4837 (1969).

MOORES, E. — Ultramafics and orogeny, with models of the U. S. cordillera and the Tethys. Nature, **228**, 837-842 (1970).

OMOGEO, P. — Distribution of the terricolous oligochaetes on two shores of the Atlantic. North Atlantic biota. (Eds. A. Love and D. Love) Pergamon, Oxford, pp. 127-152 (1963).

PACKER, D. R., STONE, D. B. — An Alaskan Jurassic palaeomagnetic pole and the Alaskan orocline. Nature Phys. Sci. **237**, 25-26 (1972).

PATTERSON, B., PASCUAL, R. — The fossil mammal fauna of South America. Quart. Rev. Biol. **43**, 409-451 (1968).

PHILLIPS, J. D., FORSYTH, D. — Plate tectonics, palaeomagnetism and the opening of the Atlantic. Geol. Soc. Amer. Bull. **83**, 1579-1600 (1972).

RIEK, E. F., — Lower Cretaceous fleas. Nature **227**, 746-747 (1970).

ROD, E. — Clues to ancient Australian geosutures. Eclogae Geologicae Helvetiae **59**, 850-883 (1966).

SAAO, A. H. — Palaeomagnetism of Franciscan ultramafic rocks from Red Mountain, California. Jour. Geophys. Research **74**, 6567-6578 (1969).

SCHARON, L., SCHARNBERGER, C., EARLY, T., SHIMOYAMA, A. — International cooperation for palaeomagnetic insight into Antarctic tectonic history. Antarctic Journal of the U. S. **5**, 219-224 (1970).

Schopf, J. M. — Ellsworth mountains: position in West Antarctica due to seafloor spreading. Science **164**, 63-65 (1970).

Schuster, R. M. — Problems of antipodal distribution in lower plants. Taxon **18**, 46-91 (1969).

Seward, A. — Plant life through the ages. Cambridge University Press (1931).

Sige, M. B. — Dents de micromammifères et fragments de coquilles d'œufs de dinosauriens dans la faune de vertébrés du crétacé supérieur de laguna Umayo (Andes Péruviennes). Comptes Rend. Acad. Sci. (Paris) **267**, 1495-1498 (1968).

Sige, M. B., — Les Didelphoidea de Laguna Umayo (formation Vilquechico, Crétacé supérieur, Pérou) et le peuplement marsupial d'Amérique du Sud. C. R. Acad. Sci. (Paris) **273**, 2479-2481 (1971).

Simpson, G. G. — The principles of classification and a classification of mammals. Bull. Amer. Mus. Nat. Hist. **85**, 1-350 (1945).

Smit, F. G. A. M. — On some adaptive structures in Siphonaptera. Folia Parasitologica (Praha) **19**, 5-17 (1972)

Smith, A. C. — The Pacific as a key to flowering plant history. University of Hawaii, Harold L. Lyon Arboretum lecture number one (1970).

Southcott, R.V., Lange, R. T. — Acarine and other microfossils from the Maslin Eocene, South Australia. Records S. Aust. Mus., **16**, 1-21 (1971).

Speoll, W. P., Dietz, R. S. — Morphological continental drift fit of Australia and Antarctica. Nature **222**, 345-348 (1969).

Takhtajan, A. — Flowering plants, origin and dispersal. Oliver and Boyd, Edinburgh (1969).

Tate, G. H. H. — Studies in the Peramelidae (Marsupialia) Bull. Amer. Mus. N. H. **92**, 313-346 (1948).

Thompson, E. O. P., Air, G. M. — Studies on marsupial proteins. VI. Evolutionary changes in β-globins of the Macropodidae and the amino acid sequence of β-globin from *Potorous tridactylus*. Aust. J. Biol. Sci. **24**, 1199-1217 (1971).

Van Balgooy, M. M. J. — Plant geography of the Pacific. Blumea, supplement **6**, 1-222 (1971).

Van Steenis, C. G. G. J. — The land-bridge theory in botany. Blumea **11**, 235-372 (1962).

Van Steenis, C. G. G. J. — *Nothofagus*, key genus of plant geography, in time and space, living and fossil, ecology and phylogeny. Blumea **19**, 69-98 (1971).

Van Steenis, C. G. G. J., Balgooy, M. M. J. — Pacific Plant Areas Vol. 2, Supplement to Blumea **5**, (1966).

Vogt, P. R. — The Faeroe-Iceland-Greenland aseismic ridge and the western boundary undercurrent. Nature **239**, 79-81 (1972).

Walden, H.W. — Historical and taxonomical aspects of the land gastropoda in the NorthAtlantic region. North Atlantic biota (Eds. A. Love and D. Love) Pergamon, Oxford p. 153 (1963).

Wellman, P., Mc Elhinny, M. K., Mc Dougall, I. — On the polar-wandering path for Australia during the Cenozoic. Geophys. J. R. astr. Soc. **18**, 371-395 (1969).

Wilson, J. T. — Static or mobile earth ; the current scientific revolution. Proc. Amer. Phil. Soc. **112**, 309-320 (1968).

Wilson, J. T., Burke, K. — Two types of mountain building. Nature **239**, 448-449 (1972).

Zuckerkandl, E. — Chemical palaeogenetics. Sci. Amer. **212**, 110-118 (1965).

DISCUSSION

Intervention du Professeur R. Hoffstetter :

Dans la communication du Dr. Martin, j'ai beaucoup apprécié la richesse de l'argumentation, le souci d'objectivité, la prudence des conclusions qui laissent la porte ouverte à diverses interprétations. Il est certain que nos informations actuelles ne permettent pas de présenter un tableau définitif de l'histoire biogéographique des Marsupiaux. Certaines hypothèses avancées (celle de Fooden p. ex.) doivent cependant être écartées, car elles contredisent des faits établis. Pour les autres, c'est essentiellement leur degré de probabilité que l'on peut comparer.

Je désirerais d'abord préciser que, selon moi, les problèmes posés par les Monotrèmes et les Marsupiaux ne relèvent pas nécessairement d'une seule et même explication. Les deux groupes dérivent respectivement de branches (Protothériens et Thériens) séparées depuis le Trias supérieur. Ni dans les faunes actuelles, ni dans les faunes fossiles en dehors de l'Australie. Un cas analogue est posé par les Reptiles néo-zélandais où l'on trouve le *Sphenodon* et quelques Geckos dont l'histoire n'est pas nécessairement liée...

Pour nous en tenir aux Marsupiaux, l'hypothèse du Dr. Martin est audacieuse et attrayante. Loyalement il reconnait lui-même qu'elle présente, elle-aussi, des points faibles. Pour ma part je lui reprocherais surtout de faire appel à une trop large part d'hypothèses, dont chacune est vraisemblable, voire même défendable, mais incontrôlable : présence d'une terre émergée sur l'emplacement de l'actuel seuil de Darwin ; peuplement de cette île par des Marsupiaux (ou des Thériens qui évoluent localement en Marsupiaux) d'origine inconnue ; partition de la même île (par le jeu d'une dorsale active dont l'existence est mise en doute par Coulomb) et migration des deux moitiés qui vont s'accoler respectivement, avec leurs Marsupiaux, à l'Amérique du Nord et à l'Australie ; arrivée de ces faunes en temps opportun pour rendre compte de la présence de Marsupiaux (associés à des Placentaires) dans un gisement albien du Texas (car, avec Slaughter, Clemens, etc... je tiens *Holoclemensia* pour un Marsupial primitif) et dans un gisement du Crétacé supérieur au sud du Pérou. Cette longue histoire exigerait une ancienneté des Marsupiaux difficilement acceptable puisque la molaire tribosphénique, inconnue au Jurassique, s'est probablement différenciée au Crétacé inférieur (voir *Aegialodon*, d'après les travaux de Crompton).

Pour ma part, je préfère serrer au plus près les faits établis. L'aire de dispersion connue des Marsupiaux actuels et fossiles comprend essentiellement l'Australie et les Amériques (et aussi l'Europe qui n'est concernée que par une brève incursion d'un genre nord-américain au cours du Tertiaire). C'est dans cette « guirlande », à laquelle il est légitime d'ajouter le maillon antarctique, qu'il convient de rechercher leur berceau (non précisé). La comparaison avec la carte du Monde au Crétacé inférieur m'a fait suggérer une différenciation des Marsupiaux et Placentaires par une ségrégation géographique due à l'ouverture des océans Indien et Atlantique. Dans cette hypothèse les Marsupiaux ont pu atteindre l'Australie (il n'est même pas exclu qu'ils aient pu y naître) avant l'arrivée des Placentaires laurasiens ; la migration de ceux-ci aurait été arrêtée par un obstacle, probablement la rupture de la guirlande quelque part entre l'Amérique du Sud et l'Australie. Les recherches paléontologiques en Antarctide permettront peut être de préciser où et quand s'est manifestée cette barrière.

De toute façon, je tiens à répéter qu'il ne s'agit, dans ce débat, que de confronter des hypothèses de travail.

Réponse du Professeur P. G. Martin :

I believe that I have already covered all the points raised by Professor Hoffstetter. In my discussion of the paper of Jardine and MacKenzie (1972) I indicated that I think the " garland " hypothesis is possible but gave reasons why I believe it is improbable. Professor Hoffstetter implies that he has faith that fossils of marsupials will be found in the Cretaceous of South America without accompanying placentals. He also implies that marsupials reached southern Australia at least fifteen million years before their earliest discovered occurrence.